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Soil mites in detrital food webs of conventional and no-tillage agroecosystems

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With 6 figures

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1. Introduction

The role of soil fauna in nutrient cycling and alteration of soil structure has only recently received attention for agroecosystems (EDWARDS *et al.* 1988). As agriculture shifts to low input and sustainable practices, our understanding of the influences of soil fauna on decomposition and nutrient cycling processes becomes increasingly important (CROSSLEY *et al.* 1989). Cultivation practices alter the composition of soil biotic communities and, in general, species numbers and diversity are greater in grassland than in plowed soils (CURRY, 1986). HENDRIX *et al.* (1986) hypothesized that decomposition processes in no-tillage agroecosystems are controlled by fungi and fungivorous soil fauna due to surface placement of the crop residues. In contrast, conventional tillage agroecosystems, in which organic debris are plowed under, may favor organisms with higher turnover rates such as bacteria and bacterivorous fauna. Furthermore, HOLLAND and COLEMAN (1987) hypothesized that fungal dominated microbial communities of no-tillage systems may store organic material for longer periods, resulting in higher steady-state levels of soil organic matter.

Soil microorganisms are probably responsible for most organic matter decay and nutrient fluxes while microarthropods probably contribute less than 10% of total soil respiration (REICHLE, 1977; PERSSON *et al.* 1980). However, exclusion studies have shown that decomposition can be significantly reduced in the absence of microarthropods (HÅGVAR, 1988; SEASTEDT, 1984). This finding has lead various authors to conclude that microarthropods are important in comminution of substrates and may accelerate decomposition rates by stimulating microbial activity (PARKINSON *et al.* 1979; SEASTEDT, 1984).

As mites are integrated into more complex models of below-ground food webs (PARTON *et al.*, 1984; HUNT *et al.*, 1984) it is increasingly important to identify their specific activities and interactions with other organisms of the food web. In many studies, soil mites are separated by taxonomic groups into the suborders Prostigmata, Mesostigmata, Astigmata and Oribatida (Cryptostigmata). It is generally assumed that Oribatida are primarily fungal feeders, Mesostigmata are predators, Prostigmata are primarily fungal feeders or predators, and Astigmata are bacterial feeders (KRANTZ, 1978; KARG, 1986; LAGERLÖF & ANDRÈN, 1988). However, these assumptions may be incorrect, since taxonomic affiliation does not necessarily reflect their trophic behavior. Some more recent studies take the trophic behavior of mites into account and reclassify them into functional groups (MOORE *et al.* 1988; WALTER *et al.* 1988).

In an experiment conducted at the Horseshoe Bend Site located in Athens, Georgia, U.S.A., the influences of different soil organisms on plant residue decomposition in conventional tillage and no-tillage agroecosystems were compared. Our objectives here were to investigate the trophic habits and temporal dynamics of soil mites and consider their interactions and coupling with saprophytic fungi in detrital food webs of conventional and no-tillage

agroecosystems. We compare findings of soil mite laboratory feeding trials with the effects of field applied fungicides on fungal and mite abundances in conventional and no-tillage agroecosystems.

2. Materials and methods

2.1. Site description

The study was conducted at the University of Georgia's Horseshoe Bend Experimental Area (HSB) near Athens, Clarke County, Georgia, USA. Except for the cropped areas, the 14 ha site is in forested or old field successional vegetation. The soil belongs to the Hiwassee series (typic Rhodudult) which is a well drained sandy clay loam containing 66 % sand, 13 % silt and 21 % clay. Details of the physical and chemical properties of these soils have been described by GROFFMAN (1985) and GROFFMAN *et al.* (1987). Four no-tillage (NT) and four conventional tillage (CT) plots, each 0.1 ha in size, have been under continuous treatment since 1978. A complete site and treatment history was provided by STINNER *et al.* (1984).

The field experiment reported here was conducted between June 1987 and May 1988. HSB usually receives 127 cm · a^{-1} of precipitation, but 1987 was very dry, and the site received only 82.6 cm of rainfall. Average daily temperature over the summer growing season ranged from 28.8 °C in July to 17.5 °C in October. The CT plots were moldboard plowed to a depth of 10 cm, disked and rotary tilled prior to planting of winter and summer crops (*Secale cereale* L., *Sorghum bicolor* L. MOENCH, respectively). In NT, the soil remained undisturbed except for planting the summer crop. The winter crop was mowed and left as green manure. Plots have received no insecticides since 1978. The herbicide glyphosphate (Roundup®, 5.5 l · ha^{-1}) was applied prior to summer planting. All plots were fertilized with 51 kg N · ha^{-1} as NH_4NO_3.

2.2. Experimental design

Two experimental plots (3 m × 3 m) were established within each of the 8 main tillage plots. One of the test plots within each tillage treatment was randomly chosen for fungicide treatment, the other was used as a control. Litterbags (10 cm × 10 cm) were made from fiberglass-nylon material with a mesh size of 1.8 mm (CROSSLEY & HOGLUND, 1962) and filled with 2.5 g of oven-dried (50 °C) winter rye (*Secale cereale* L.) litter collected at senescence from HSB. The litterbags were randomly placed in the experimental plots. One half of the litterbags were buried in a vertical slit made with a shovel. The other half were laid on the soil surface (CT) or positioned under a layer of fresh rye litter (NT).

The fungicide Captan (17.5 g m^{-2}) was applied to designed experimental plots in suspension form (4.5 l H_2O · m^{-2}). This amount was previously determined to achieve the greatest inhibition of the target group and minimize non-target or direct chemical effects (BEARE, 1989). Control plots received the same amount of H_2O (4.5 l · m^{-2}). Captan treatments were applied about every 6 weeks, since the fungicide volatilizes rapidly after application (INGHAM & COLEMAN, 1984). Field samples were taken at 2, 6, and 14 d following each application. One surface and one buried litterbag were collected from each plot on each sample data for microarthropod extractions and measurements of mass loss (n = 4 for each tillage by fungicide treatment). An additional set of litterbags was collected as above (n = 4) for fungal enumerations.

Mites were extracted from litterbags on modified Tullgren funnels for 72 h. Individuals were initially identified to the suborders Prostigmata, Mesostigmata, Astigmata and Oribatida and were subsequently identified to family level. Immediately after extraction, the litter was oven-dried for 48 h (50 °C) to obtain dry mass used for the calculation of decomposition rates. Litter was ground in a Wiley mill to pass a 40 mesh screen (160 µm). Ash free dry mass (AFDM) was determined from 500 mg litter subsamples ashed at 500 °C for 4 h. Daily decay constants (k) were calculated from soil corrected percent mass remaining data (BLAIR & CROSSLEY, 1988) using the single negative exponential decay function (LN [collected mass/initial mass] = − kt) after OLSON (1963).

A second set of litterbags were used to measure fungal hyphal lengths and litter moisture content. A subsample was removed from the bag to record wet mass and dry mass (oven dried at 60 °C for 48 h). Another subsample (0.4−0.8 g dry mass) was taken field moist, diluted with filtered autoclaved water (40−60 ml) and homogenized for 60 s at low speed in a Virtis blender. From appropriate dilutions of the homogenates, enumerations of total fungal hyphal lengths (JONES & MOLLISON, 1948) were made on a Zeiss (IM 35) photomicroscope.

2.3. Laboratory experiments

Laboratory studies were conducted to observe feeding habits of the common microphytophages and predatory mites found in the NT and CT plots. Live extractions of the families Oribatulidae, Oppiidae, Nothridae, Galumnidae, Microzetidae, Tectocepheidae, Haplozetidae (Oribatida), Uropodidae, Laelapidae, Macrochelidae (Mesostigmata), Cunaxidae, Eupodidae, Tydeidae, Pygmephoridae, Tarsonemidae and Scutacaridae (Prostigmata) were made from soil and litter field samples. The samples were placed on modified Tullgren funnels and mites were extracted into plastic containers one-third filled with a 10 : 1 mixture of plaster of Paris and charcoal. Mites of different families were kept in separate containers and offered different diets consisting of either bakers yeast, laboratory grown fungi (Basidiomycetes), bacterivorous (Rhabditida) or fungivorous *(Aphelenchoides sp.* and *Aphelenchus sp.)* nematodes, soft bodied Astigmata mites (Acaridae) or Collembola (Onychiuridae and Isotomidae). Observations on feeding attempts and general behavior, egg production, successful development to adult stages and successful reproduction over more than one generation were recorded.

3. Results

3.1. Mite trophic classifications and dynamics

The feeding behaviour of common mite families from the HSB site in laboratory cultures are summarized in table 1. Results of the laboratory experiments revealed considerable variability in the trophic behavior of mite families from the different suborders. The Prostigmata include the exclusively predatory Cunaxidae as well as the fungivorous Tarsonemidae. Most members of the soil Mesostigmata, such as the families Laelapidae and Macrochelidae are predators, but classification of a Uropodidae species commonly found at HSB was more difficult. While these mites would survive over several months on a diet of yeast or nematodes, they would only reproduce in the presence of fungi. Even more diverse was the feeding behavior of many families

Table 1. Feeding observations of common mite families from the HSB site in laboratory cultures and additional observations for these families from the literature.

Family	Fungi	Yeast	Nematodes	Mites	Collembola	Algae
Oribatida						
Oribatulidae	++++	+++	++		+	W[1]
Oppiidae	++++	+++				
Haplozetidae	+++	++	++			W[1]
Galumnidae sp1	++	++	++	+	++	W[2]
Galumnidae sp2	+	+				
Nothridae		+				
Tectocepheidae	W[1]	+				W[1]
Prostigmata						
Tarsonemidae	++++	+++				W[1]
Eupodidae	+++					W[2]
Tydeiidae	W[2]					W[2]
Scutarcaridae	W[3]					
Pygmephoridae	W[3]					
Cunaxidae		++++	++++	+++		
Mesostigmata						
Uropodidae	++++	+++	+++			
Laelapidae			++++	++++	++++	
Macrochelidae			++++	+++	+++	
Ascidae			++++	++++	++++	

+ = occasional feeding; ++ = more frequent feeding; +++ = reared to adult stage; ++++ = reared over more than one generation; W[1] = WALTER, 1987b; W[2] = WALTER *et al.*, 1988; W[3] = WALTER, 1987a

of Oribatida. Oribatulidae were very easy to rear on a fungal diet over many generations, but occasionally fed on Collembola or nematodes when fungi were not provided. It is difficult to determine if this behavior in the laboratory reflects the behavior of mites in the field. One of the Galumnidae species (Gen. sp. 1) was observed to feed frequently on nematodes and Collembola as well as on fungi, but would not reproduce in the laboratory.

These observations, together with descriptions from the literature, led to the regrouping of the mites into Fungivores, Predators and 'Other'. Fungivores included the Oribatulidae, Oppiidae, Haplozetidae, Tarsonemidae, Galumnidae (Gen. sp. 1), Eupodidae, Tydeidae, Uropodidae. Predators included Cunaxidae, Laelapidae, Macrochelidae and Ascidae. Uncommon families and those with unknown feeding habits, such as Scutacaridae, Tectocepheidae or Pygmephoridae, were defined as 'Other'.

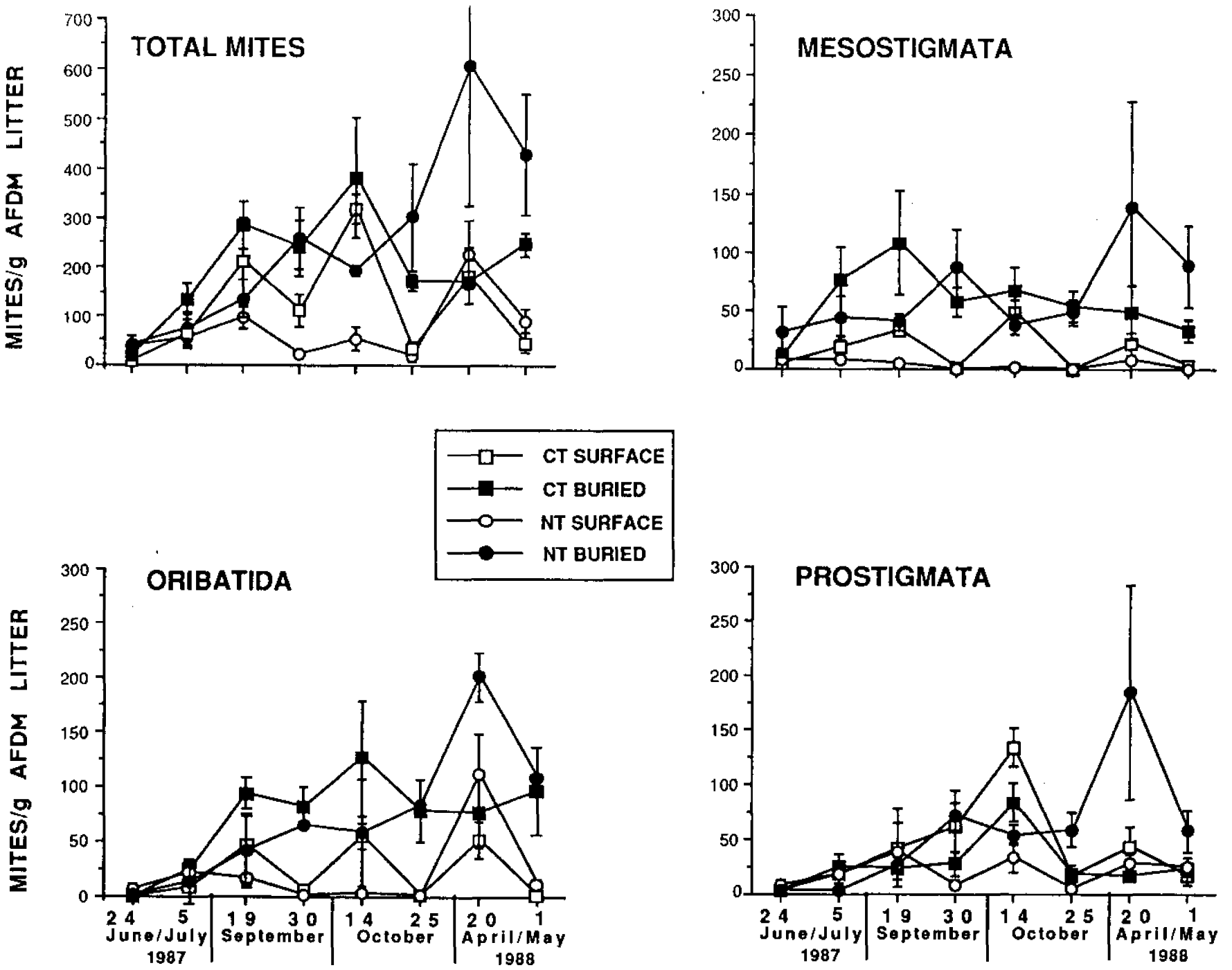

Fig. 1. Mean numbers (± 1S.E.) of total mites (adults plus immatures) and adult Oribatida, Mesostigmata and Prostigmata in surface and buried litter from CT and NT agroecosystems over the 10 month study period.

Fig. 1 shows the abundances of mites from litterbags based on the traditional separation into suborders. Buried litter usually had higher total mite numbers than surface litter. Overall mean densities of mites were found to be positively related to decomposition rates. Total mites reached their highest abundances in NT buried litter followed by CT buried litter, which had decay rate constants (k) of $-0.0058\,d^{-1}$ and $-0.0026\,d^{-1}$, respectively. The lowest abundances of mites were found in NT surface and CT surface litter, which had decay rate constants (k) of $-0.0021\,d^{-1}$ and $-0.0018\,d^{-1}$, respectively. Colonization of CT buried litter by Mesostigmata and Oribatida mites was generally faster than for NT buried litter.

After soil mites were reclassified into functional groups, the dominance of fungivorous mites in litter became apparent (fig. 2). Numbers of fungivorous mites increased more slowly in NT buried litter than in CT buried litter, but the highest population density in NT was found in spring

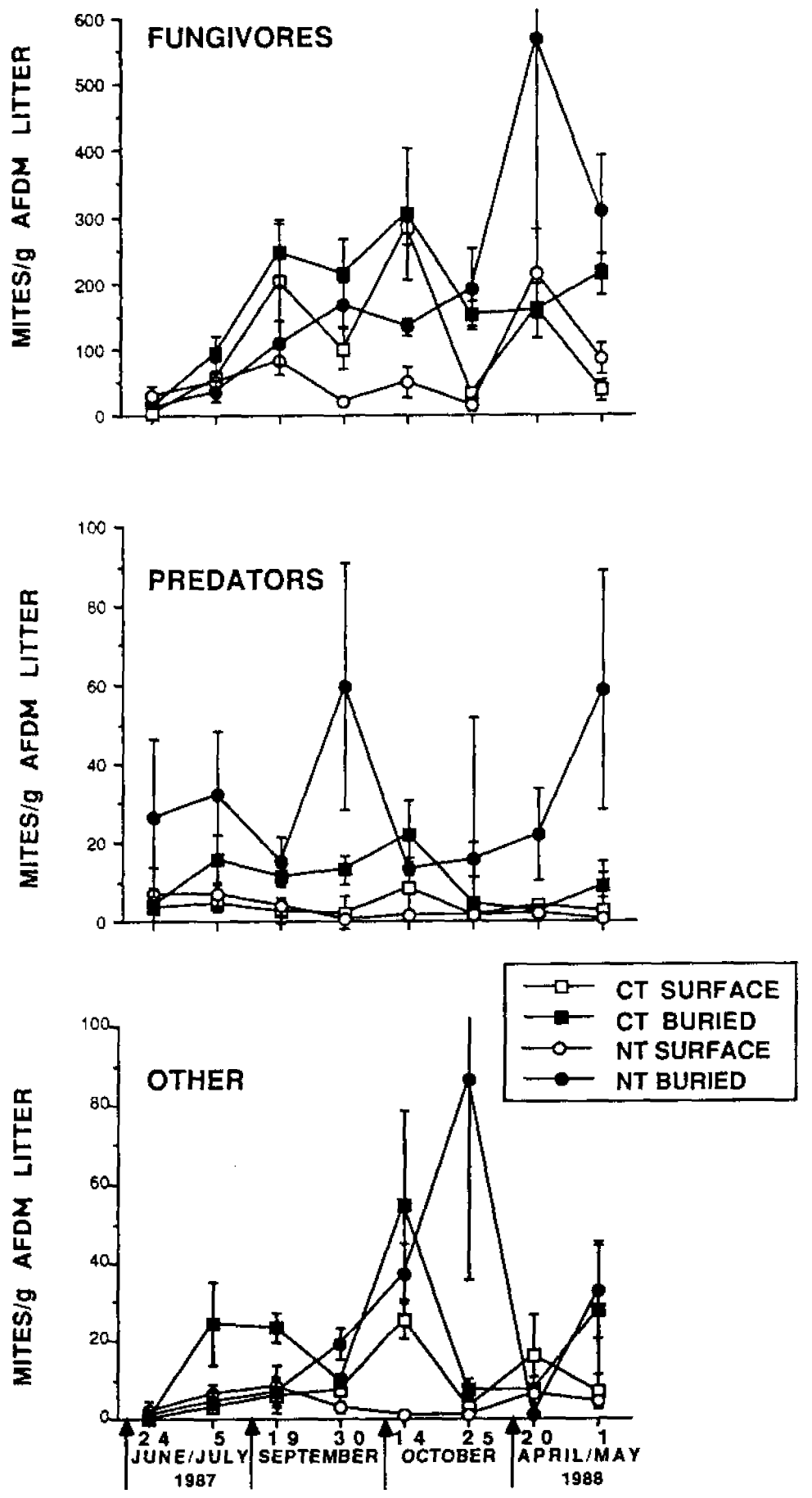

Fig. 2. Mean numbers (± 1S.E.) of adult fungivore, Predators and 'Other' mites in surface and buried litter from CT and NT agroecosystems over the 10 month study period.

1988 when numbers in CT buried litter had already declined. Predators were more abundant in NT buried litter than in any other treatment. The numbers of mites grouped as 'Other' showed a steady increase in NT buried litter through the last sampling date in October. In CT buried litter the colonization was faster, but numbers decreased earlier in the study. Surface litter was evidently not a preferred habitat for both predators and 'Other' mites.

A comparison of the taxonomic (suborder) and functional group classifications is shown in table 2 based on overall mean densities of mites within each tillage and placement treatment. This table illustrates the potential inadequacies of assumptions about trophic affiliations, based on suborders. The percentage distribution of the suborders did not correlate well with that of the functional groups. Oribatida (considered as fungivores) made up a considerably lower percentage of the total mite community in CT surface as compared to CT buried litter. Mesostigmata were much less common in NT surface, while Prostigmata were poorly represented in CT buried litter. Fungivorous mites made up 85 to 90 % of the total mite communities regardless of tillage or litter placement; however, Prostigmata plus Oribatida (generally considered fungivores) made up between 64 and 91 % of the communities. Within tillage treatments, predatory mites made up a considerably larger proportion of the total mite community in buried litter than in surface litter. The percentage of 'Other' mites was lowest in NT buried litter, similar in NT and CT surface litter and highest in CT buried litter.

Table 2. Average percent distribution of mite groups on surface and buried litter from CT and NT agroecosystems.

	CT surface	CT buried	NT surface	NT buried
Suborders				
Prostigmata	52.73	17.68	45.04	29.79
Oribatida	26.74	46.69	46.28	37.03
Mesostigmata	20.52	36.23	8.68	33.18
Functional groups				
Fungivores	90.06	85.48	89.80	84.70
Predators	2.98	5.01	4.78	13.48
Other	6.97	9.42	5.42	1.82

Mite suborder and functional group classifications are shown for comparison.

3.2. The fungal link

The field studies with Captan were designed to examine interactions between fungi and fungivorous mites in the detrital food webs. Captan is a N-trichloromethylthio-4-cyclohexane-1,2-dicarboximide fungicide with a relatively wide spectrum for inhibition of saprophytic fungi. Captan reacts with the functional group of thiol in the cell to produce thiophosgene (LUKENS, 1971). Captan significantly ($p < 0.05$) reduced total fungal hyphal lengths in surface and buried litter from both NT and CT plots on most sample dates (fig. 3). Overall mean densities of fungal hyphae were significantly greater in NT surface litter than in CT surface litter ($p < 0.05$). Hyphal

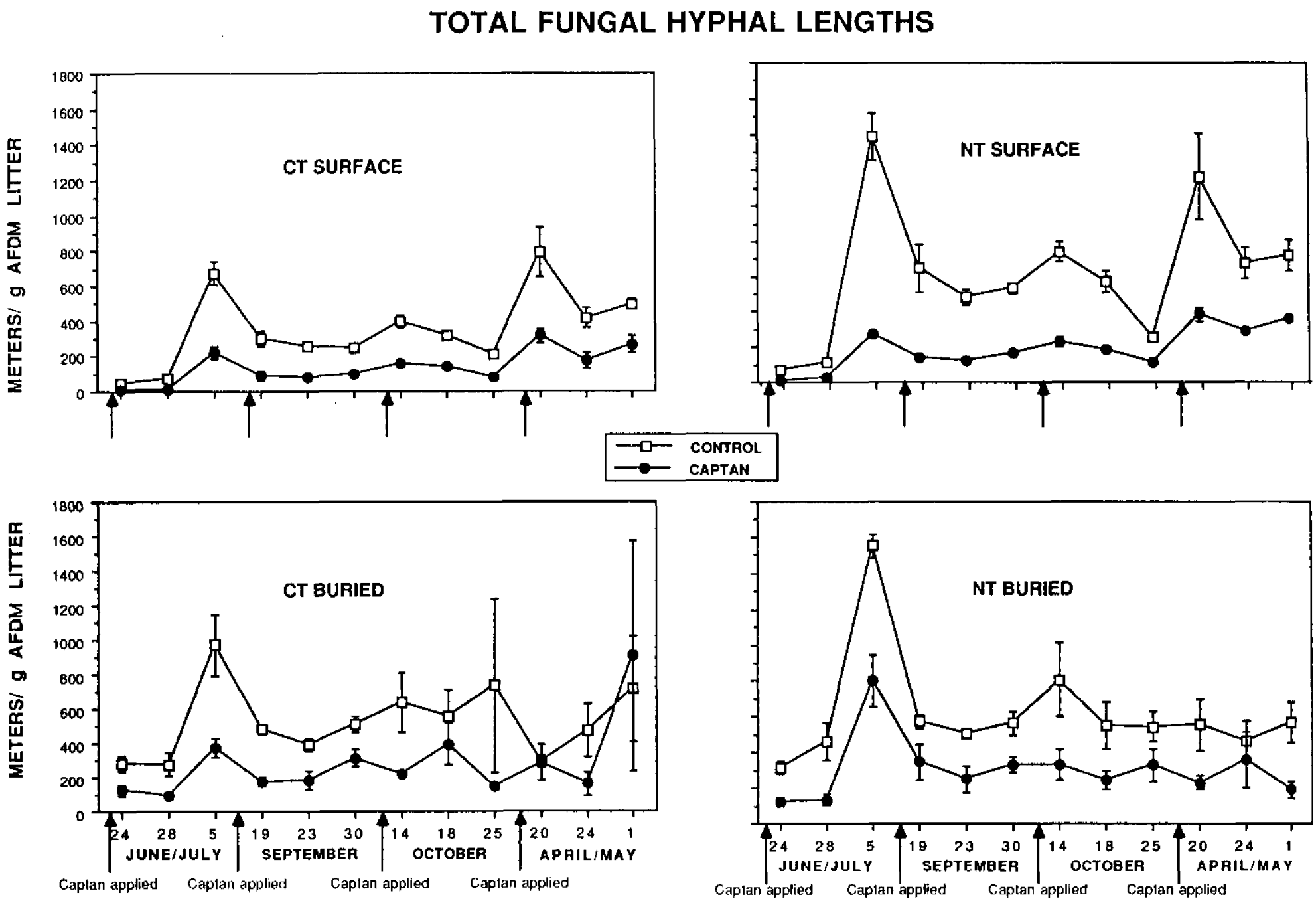

Fig. 3. Mean lengths (± 1S.E.) of total fungal hyphae in surface and buried litter from captan and control treatments in CT and NT agroecosystems over the 10 month study period. Arrows indicate applications of Captan.

abundances peaked after 26 d in the field; subsequently, their densities in buried litter remained fairly constant throughout the remainder of study. In surface litter, densities increased again in spring of 1988.

The effect of fungal reductions by Captan on mite abundances differed among families. Figs. 4 and 5 show changes in the abundances of the 3 most common Oribatid families (Oribatulidae, Haplozetidae, Oppiidae) and the Prostigmatid family Tarsonemidae, which we consider predominantly fungivores. Abundances of Oribatulidae, Oppiidae, Haplozetidae and Tarsonemidae were reduced in NT buried litter from the Captan treatments relative to the controls. Oribatulidae, Tarsonemidae and Haplozetidae also followed this trend in CT surface litter. In NT buried litter, densities of all four families generally increased over the study period. Mite abundance often peaked on the first sample date following each reapplication of water or Captan. In NT surface litter, Oribatulidae and Haplozetidae had peak densities on the first sampling date in spring 1988. Abundances of Oribatulidae and Oppiidae in CT surface litter fluctuated considerably over the study period.

Mites of the family Nothridae were strongly influenced by litter placement (fig. 6). Nothridae were absent from surface litter except on the first sampling date in spring 1988, but were considerably more common on buried litter from both tillages. Colonization of litterbags by this family was very slow and numbers suddenly increased on the last sampling date, almost a year after the litter was placed in the field. Attempts to culture Nothridae on a fungal diet were not successful; however, numbers were reduced in NT buried litter from the Captan treatments. Attempts to culture Tectocepheidae on a fungal diet were also not successful. The Captan treatment actually caused an increase of Tectocepheidae in NT surface litter, suggesting that fungi may not be an important part of their diet or that they may prefer dead or senescent fungal hyphae.

4. Discussion

The role of microarthropods in below-ground detrital food webs has recently been discussed in connection with the reclassification of microarthropods into functional groups. MOORE *et al.* (1988) have classified the arthropods of the below-ground food web into the functional groups of Predators, Microphytophages, Detritivores, Phytophages and Omnivores, where the functional groups do not correspond to taxonomic ones. Other authors have questioned the reality of trophic levels for soil organisms. WALTER (1987a, 1988) and WALTER *et al.* (1986, 1988) have made several detailed studies on feeding behaviors of mites from semiarid grassland sites and found that some previously reported mycophagous species will feed at more than one trophic level and occasionally or regularly include fauna, such as nematodes, in their diets. Under laboratory conditions many of the microphytophagous families in this study were also observed to feed on nematodes or other microarthropods. WALTER (1987b) discussed the occurrence of predatory behaviour by microphytophages and suggested that members of this group be classified as omnivorous.

In defining an organism trophically, it seems more important to recognize the food source which is essential for reproduction of a species, since both food availability and quality control reproduction and turnover rates. However, there may be cases where these food sources make up a small percentage of an organism's diet. Furthermore, predatory behavior under field conditions must be rather difficult for many of the mycophagous species, since their locomotion and mouth parts are not appropriate for predatory feeding. The mite trophic classification scheme presented here was based primarily on these criteria. Many of the mycophagous families defined from our laboratory studies were observed to feed at several trophic levels; however, a fungal diet was required for most to reach adult stages and for successful reproduction. Furthermore, when saprophytic fungi were inhibited in the field with captan, densities of fungivorous mites also declined, in at least some treatments, relative to controls. These findings support the laboratory based trophic classification of these organisms and suggest tight coupling between fungi and fungivorous mites in these agroecosystems.

The greatest effects of fungal inhibition on fungivorous mites were observed in NT buried litter and CT surface litter. These placements of litter are unusual for these tillage treatments and

thus they may have functioned as somewhat isolated islands for fungal and faunal colonization. These islands may have amplified the effects of fungal inhibition (Captan) on soil mites, since these isolated subtrates may serve as sites of concentrated mite activity. This hypothesis is supported by the evidence that densities of Oribatulidae, Haplozetidae, Oppiidae and Tarsonemidae were often greater on CT surface and NT buried litter than on NT surface and CT buried litter, respectively.

The occurrence and distribution of soil mites in agroecosystems and their interactions with other soil organisms depends on a variety of environmental conditions. A primary factor is the microclimate. PERDUE and CROSSLEY (1990) concluded that microclimatic factors exert an important influence on Acari population dynamics in agroecosystems. In this study, the influence of microclimatic factors on mite densities was most obvious in CT surface litter. Abundances of Oribatulidae, Haplozetidae and Tarsonemidae reached a peak after each application of water in the control plots, a trend which is not as apparent in NT, where the litter layer provides better protection under drought conditions.

The colonization of litter by soil biota at the two placements (surface versus buried litter) is likely influenced by differences in the imposed microclimatic conditions and by the effects of tillage on soil structure. Despite similar densities of fungi on surface and buried litter, total mite abundances were greater on buried litter than surface litter, regardless of tillage. Estimates of mite abundances may not reflect their importance in agroecosystems. However, our laboratory studies showed that mites of the families Oribatulidae and Oppiidae grazed heavily on fungi and, although moderate fungivore feeding can increase fungal activity, overgrazing tends to reduce fungal growth and activity (HANLON, 1981). Thus, the high densities of fungivorous mites on buried litter may account for the lower than expected densities of fungal hyphae in these samples. Although close relationship between numbers of mites and fungal densities were not obvious, overall mean densities of mites were positively related to litter decay rate constants. HÅGVAR (1988) has shown from exclusion studies that decomposition decreased in absence of microarthropods. In this study, the highest abundances of fungivorous (especially Oribatulidae, Oppiidae and Tarsonemidae) and predatory mites occurred in NT und CT buried litter, where decomposition rates were greatest.

Tillage (conventional versus no-tillage) may also be an important factor regulating the colonization of litter by soil mites. In general, fungivorous mites were quicker to colonize buried and surface litter of CT than NT. Despite these observations, high densities of mites were obtained from buried litterbags of NT during the study period. Population densities of fungivorous mites increased more slowly in buried litterbags from NT than CT, possibly due to the differences in soil structure. HOUSE *et al.* (1984) compared soil structure in the 2 tillage treatments and described the no-tillage soil as stratified in contrast to CT. This stratification of NT soils may have served as an impediment to early colonization of NT buried litter. Some mixing of organic material into the subsoil of NT may be accomplished by soil biota, such as earthworms, insects or microarthropods and the colonization of NT buried litter by fungivorous mites in spring of 1988 seems to correspond with periods of peak soil faunal activity.

Our findings suggest that fungivory may be a dominant trophic habit of mites from these agroecosystems. However, many of these mites are at least capable of feeding at other trophic

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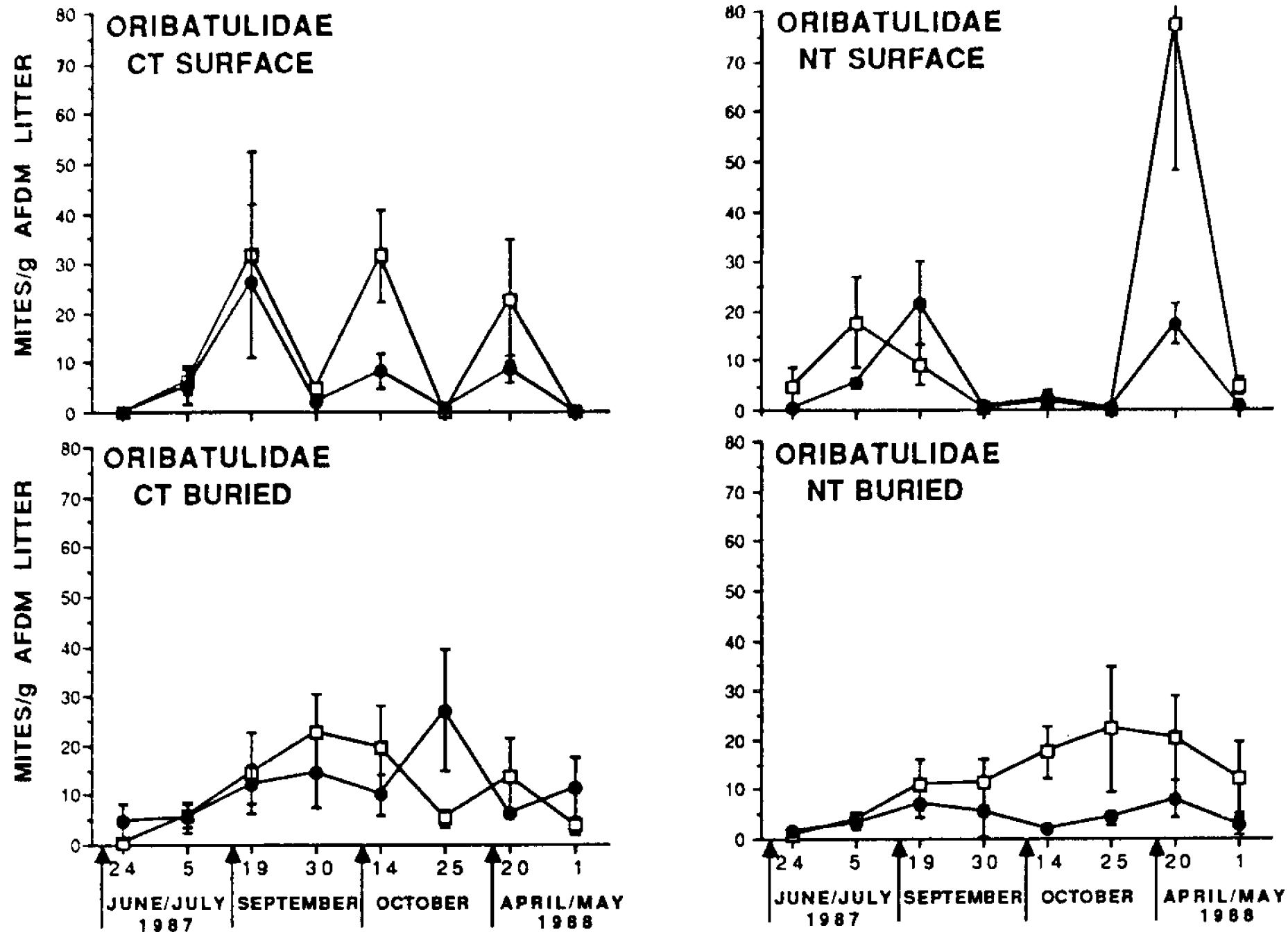
Fig. 4. Mean numbers (± 1S.E.) of adult Oribatulidae and Haplozetidae in surface and buried litter from Captan and control treatments in CT and NT agroecosystems over the 10 months study period. Arrows indicate applications of Captan.

Fig. 5. Mean numbers (± 1S.E.) of adult Oppiidae and Tarsonemidae in surface and buried litter from Captan and control treatments in CT and NT agroecosystems over the 10 month study period. Arrows indicate applications of Captan.

Fig. 6. Mean numbers (± 1S.E.) of adult Nothridae and Tectocepheidae in surface and buried litter from Captan and control treatments in CT and NT agroecosystems over the 10 month study period. Arrows indicate applications of Captan. Erratum: TECTOCEPHEDEIDAE should be read TECTOCEPHEIDAE.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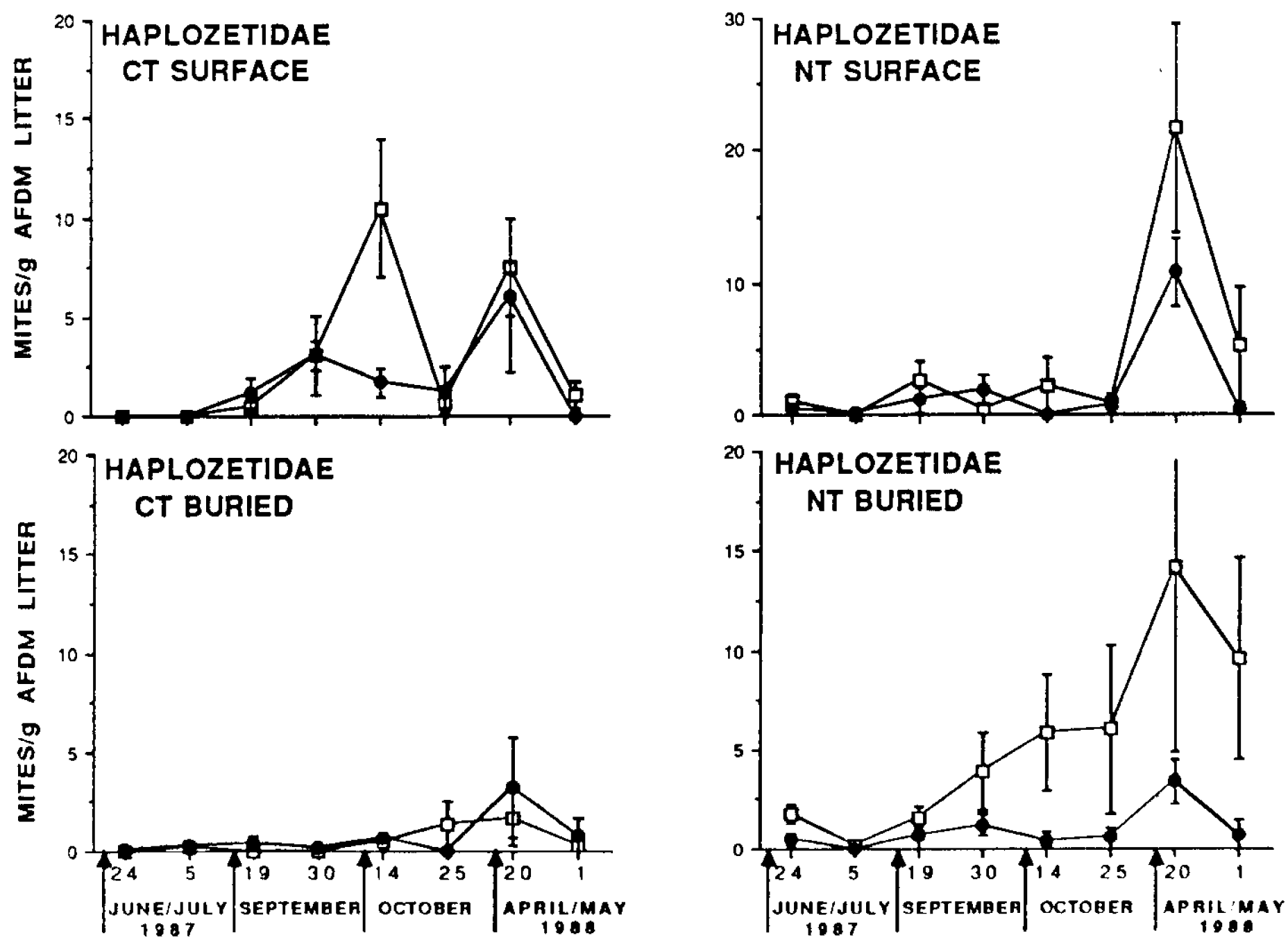
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Fig. 4

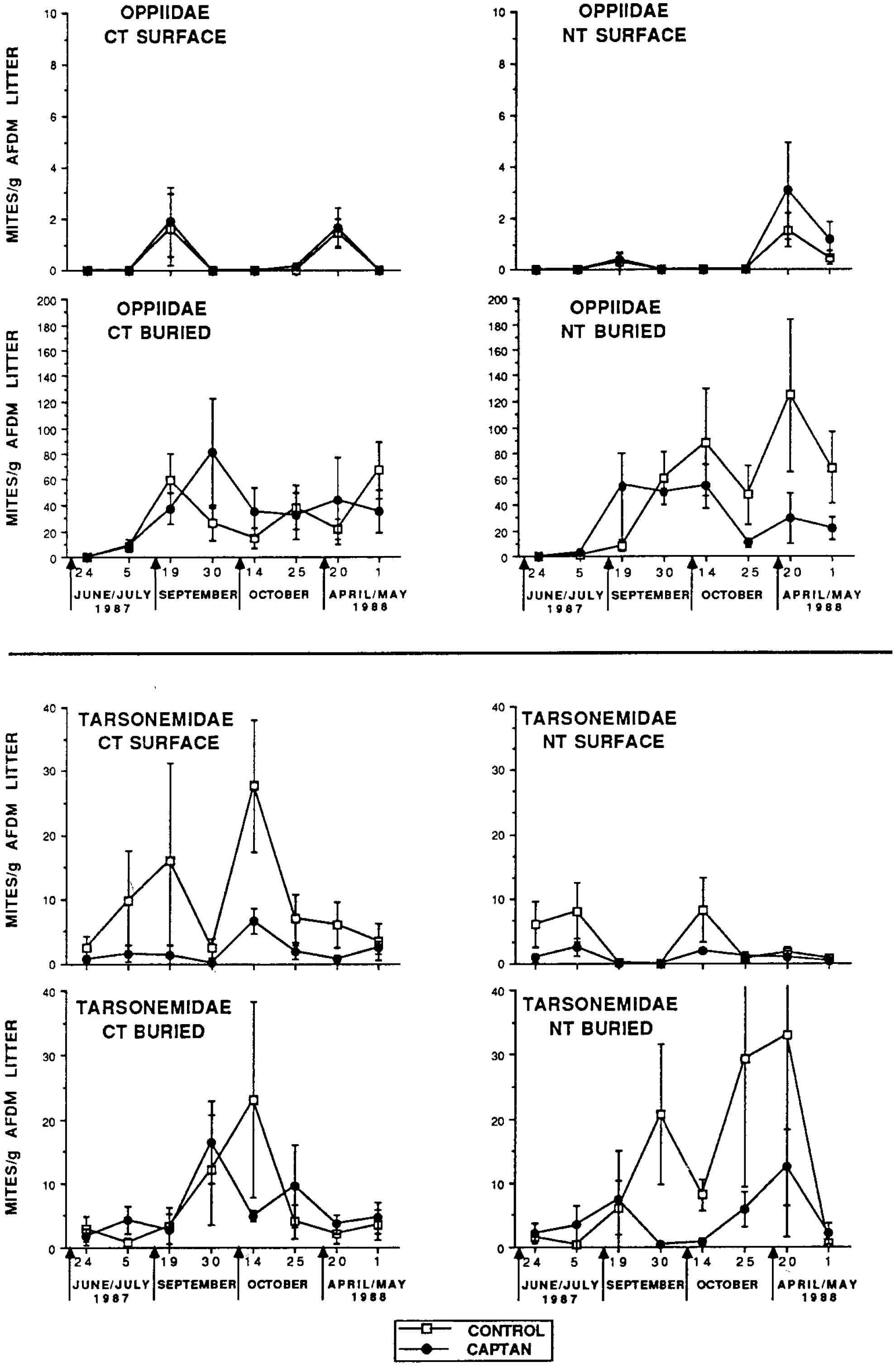
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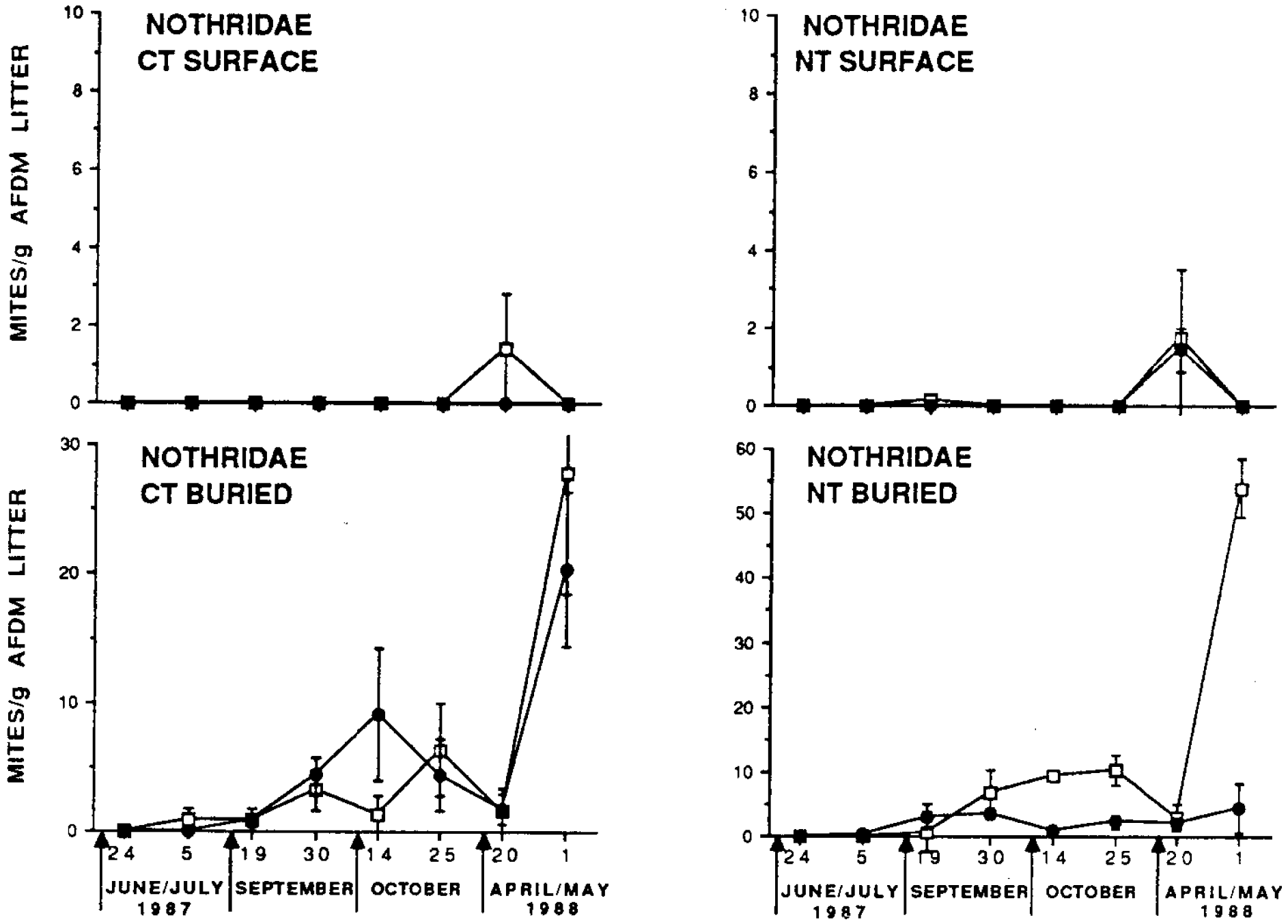
Fig. 5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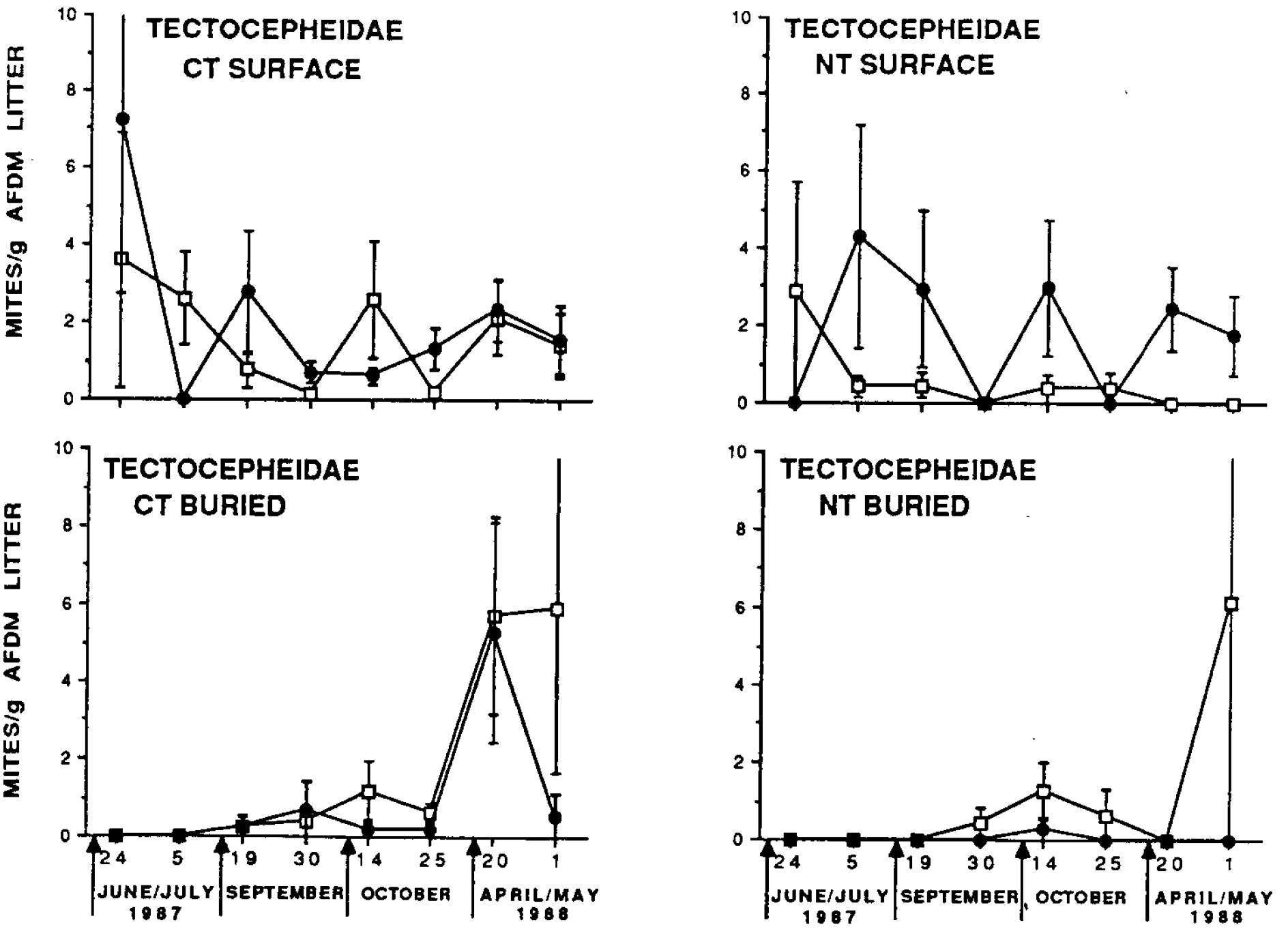
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Fig. 6

levels. As a result, many interesting questions remain: Do omnivorous mites have and use different enzymes to digest their prey and does the cost and benefit of producing those enzymes constitute an advantage over more specialized species? Inquiry into the importance of omnivory in soil ecosystems remains interesting, and new findings may shed additional light upon the validity of conventional foodweb theory for below-ground systems.

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Field and laboratory studies were initiated in June, 1987 to investigate the feeding habits and temporal dynamics of litter mites from conventional and no-tillage agroecosystems. Experimental manipulations of saprophytic fungi with the fungicide Captan in the field were used to investigate the interactions and coupling of mites and fungi in detritus food webs of these systems. Applications of a functional trophic classification, based on laboratory feeding trials, indicated the dominance of fungivory in litter from both agroecosystems as compared to the traditional suborder classification. Predatory mites made up a considerably larger proportion of the total mite communities on buried litter than surface litter from both tillages. Captan strongly reduced fungal hyphal densities on surface and buried litter from both tillage treatments over the study period. The dominant fungivore mite families (Oribatulidae, Oppiidae, Haplozetidae and Tarsonemidae) were also reduced in Captan treated litterbags as compared to controls, suggesting tight coupling between fungi and fungivore mites in these agorecosystems.

Key words: Soil mites, trophic habits, fungivory, captan, agroecosystems, litter decomposition, detritus food webs.

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